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Molecular cytogenetic analysis of *Agropyron elongatum* chromatin in wheat germplasm specifying resistance to wheat streak mosaic virus

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Summary. Three lines derived from wheat (6x) × *Agropyron elongatum* (10x) that are resistant to wheat streak mosaic virus (WSMV) were analyzed by chromosome pairing, banding, and in situ hybridization. Line CI15321 was identified as a disomic substitution line where wheat chromosome 1D is replaced by *Ag. elongatum* chromosome 1Ae-1. Line 87-94-1 is a wheat-*Ag. elongatum* ditelosomic addition 1Ae-1L. Line CI15322 contains an *Ag. elongatum* chromosome, 1Ae-2, that substitutes for chromosome 1D. The short arm of 1Ae-2 paired with the short arm of 1Ae-1 at metaphase I (MI) in 82% of the pollen mother cells (PMCs). However, the long arms of these two chromosomes did not pair with each other. In CI15322, the long arm of chromosome 4D has an *Agropyron* chromosome segment which was derived from the distal part of 1Ae-1L. This translocation chromosome is designated as T4DS·4DL-1Ae-1L. T4DS·4DL-1Ae-1L has a 0.73 μm distal part of the long arm of 4D replaced by a 1.31 μm distal segment from 1Ae-1L. The major WSMV resistance gene(s) in these lines is located on the distal part of 1Ae-1L.

Key words: Wheat – *Agropyron elongatum* derivatives – WSMV resistance – Molecular cytogenetics

Introduction

Wheat streak mosaic (WSM) is an important virus disease in the Great Plains of the United States and Canada as well as in many other wheat-producing countries of the world. Loss in yield due to WSM in Kansas was estimated at 13%, or 42 million bushels, in 1988 and has averaged 2.5% from 1976 to 1988 (Sim et al. 1988). No wheat variety is resistant to this disease. Limited tolerance is found in some wheat varieties but even these may be severely damaged in some years (Martin et al. 1976). High levels of resistance to wheat streak mosaic virus (WSMV) and its vector, the wheat curl mite (*Aceria tulipae* Keifer), are found in several genera among the Triticeae, including *Secale*, *Agropyron*, and *Elymus* (McKinney and Sando 1951; Sill et al. 1964; Somsen and Sill 1970; Sharma et al. 1984; Stoddard et al. 1987a, b).

WSMV-resistant germplasm was developed from crosses between wheat and *Agropyron intermedium* (Host) P.B. (= *Thinopyrum intermedium*, 2n = 6x = 42) (Lay et al. 1971; Wells et al. 1973; Liang et al. 1979; Wells et al. 1982). The resistance gene was located on the short arm of an *Ag. intermedium* chromosome (Wang and Liang 1977) designated as 4Ai-2 (Friebe et al. 1991). WSMV-resistant germplasm was also derived from wheat × *Agropyron elongatum* (Host) Beauv. (= *Lophopyrum ponticum*, 2n = 10x = 70) crosses. Larson and Atkinson (1970) reported a triple alien substitution line that was immune to WSMV. Later it was shown that an *Ag. elongatum* chromosome, 6Ag, conferred resistance to colonization by the wheat curl mite (Larson and Atkinson 1973). Wheat-*Ag. elongatum* chromosome translocation lines involving 6Ag were also produced (Whelan et al. 1983; Whelan and Hart 1988).

Sebesta and Bellingham (1963) reported that a 46-chromosome plant, P_3-19, derived from wheat × *Ag. elongatum*, was highly resistant to WSMV. Two 42-chromosome lines (CI15321 and CI15322) derived

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from P_3-19 were released as germplasm because of their potential value for improving WSMV resistance in wheat (Sebesta et al. 1972). Several reports showed that these two lines were highly resistant to both WSMV and its vector (Martin et al. 1976; Pfannenstiel and Niblett 1978). In the present paper, we report on the chromosome constitution and cytogenetic identification of *Ag. elongatum* and the wheat-*Ag. elongatum* translocation chromosomes of CI15321 and CI15322.

Materials and methods

Three WSMV-resistant lines derived from wheat × *Ag. elongatum* crosses were analyzed in this study. CI15321 and CI15322 are 42-chromosome wheat × *Ag. elongatum* derivatives developed at Stillwater, Oklahoma (Sebesta et al. 1972). These lines were derived from a line P_3-19 (2n = 46) developed by W. J. Sando (USDA) from a complex hybrid: *Triticum* sp. × *Ag. elongatum* (Host) Beauv. × [(Arlando × *T. timopheevii* Zhukov.) × (Hope × Baart)] × Nebred. P_3-19 was crossed with wheat cultivar 'Wichita' and a 44-chromosome plant resistant to WSMV was selected from an F_3 population. Plants from irradiated seeds of the 44-chromosome plant were again used as males in crosses with 'Wichita'. Martin et al. (1976) reported that CI15321 is a chromosome substitution line, while CI15322 is a chromosome translocation line although no data or references were cited in support of their conclusions.

We developed a WSMV-resistant line, which we designated as 87-94-1, from CI15321 × wheat cultivar 'Eagle' in the F_4 generation. This line was found to be a ditelosomic addition line with 2n = 42 + 2t chromosomes.

For meiotic pairing analysis, anthers at the metaphase I (MI) stage of meiosis were collected and fixed in a 3:1 solution of ethanol:glacial acetic acid for 3–5 days, and squashed in 1% acetocarmine. The N-banding and C-banding techniques were performed using the methods described by Gill et al. (1991). The in situ hybridization protocol was according to Rayburn and Gill (1985). The ribosomal gene probe consisted of plasmid pUC8 containing a single wheat 18*s*-26*s* rRNA gene repeat unit obtained from plasmid pTa71 (Gerlach and Bedbrook 1979). The genomic in situ hybridization (GISH) followed published procedures (Le et al. 1989; Mukai and Gill 1991). The lengths of 20 chromosomes were measured following C-banding and genomic in situ hybridization. To compare measurements, the length of chromosome 3B was determined and data were given as a percent of the total 3B length. Positions of breakpoints were calculated as a fraction of the total chromosome arm length from the centromere (fraction length, FL).

Results

Designation of chromosomes

The *Ag. elongatum* genome (2n = 10x = 70) has seven homoeologous or homologous groups of ten chromosomes each. Since the genomic origin of each chromosome within a group is unknown, we will designate them as 1Ae-1, 1Ae-2,...1Ae-10, representing the ten chromosomes of homoeologous or homologous group 1 of *Ag. elongatum* (see also Friebe et al. 1991).

Chromosome constitution of CI15321

A C-banded mitotic metaphase of CI15321 is shown in Fig. 1a. Chromosome 1D is missing in this line and is substituted with an *Ag. elongatum* chromosome designated 1Ae-1 because it compensates for the loss of chromosome 1D of wheat. Chromosome 1Ae-1 has a distinctive C-banding pattern with telomeric bands on both arms and two faint interstitial bands in the short arm.

The results of C-banding analysis were confirmed by meiotic pairing analysis. In an F_1 plant between 'Chinese Spring' nulli 1D-tetra 1B and CI15321, the expected types of chromosome pairing were observed (Table 1), i.e., 1I + 19II + 1III (Fig. 2a) or 2I + 20II. The univalent chromosome in the first configuration has to be chromosome 1Ae-1.

GISH further confirmed that chromosome 1Ae-1 was derived from *Ag. elongatum* (see Fig. 3).

Chromosome constitution of 87-94-1

Line 87-94-1 was derived from the cross of CI15321 × 'Eagle' wheat and its somatic chromosome number is 2n = 42 + 2t (Fig. 1b). C-banding analysis showed the banding pattern of the telocentric chromosome to be identical to the long arm of chromosome 1Ae-1 of line CI15321 (see Fig. 3). Wheat chromosomes 1D is present in 87-94-1.

In the F_1 plants of 87-94-1 × CI15321, chromosomes paired as 1I + 21II (Table 1), including a heteromorphic bivalent involving one chromosome and one telosome (Fig. 2b). This result confirmed that the telocentric chromosome was derived from the long arm of 1Ae-1 in CI15321 and can be designated 1Ae-1L.

GISH analysis showed that only the telocentric chromosomes in 87-94-1 originated from *Ag. elongatum* (Fig. 3).

Chromosome constitution of CI15322

C-banding analysis revealed that chromosome 1D is also replaced by an *Ag. elongatum* chromosome in CI15322 (Fig. 1c). This *Ag. elongatum* chromosome, designated 1Ae-2, is about 5.05 μm long (Table 2). It is smaller than 1Ae-1 (5.46 μm) present in CI15321, and differs from 1Ae-1 in C-banding pattern. Telomeric bands are present on both arms. The band located in the long arm is larger than the one in the short arm. In addition, two faint subtelomeric bands are located on the long arm of this chromosome. The difference between 1Ae-1 and 1Ae-2 was further revealed by in situ hybridization using the ribosomal gene probe. Ribosomal genes were located on the terminal part of the long arm of 1Ae-2 (Fig. 3), whereas no signal was detected on chromosome 1Ae-1.

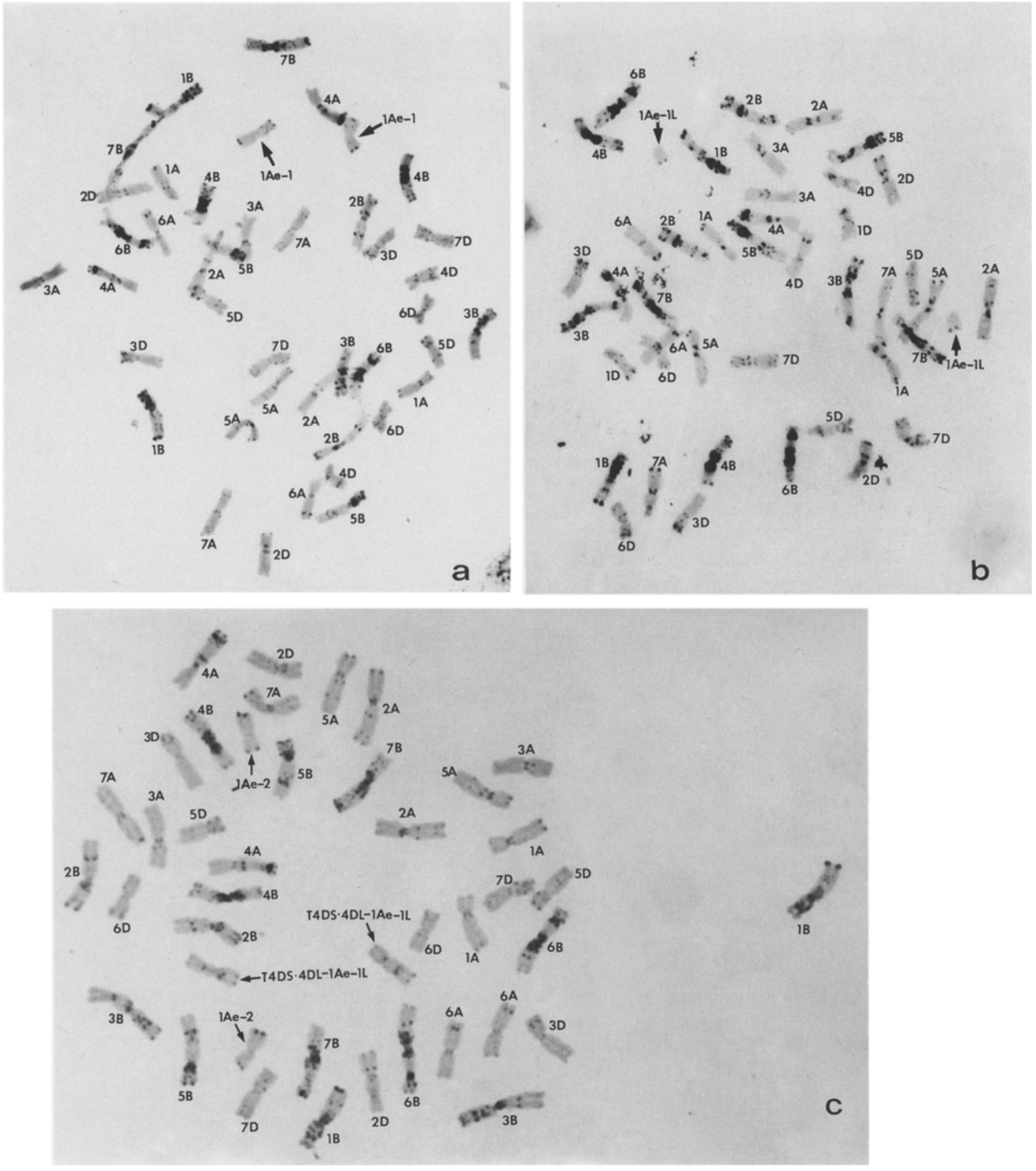

Fig. 1a–c. C-banded mitotic metaphases of WSMV-resistant lines: **a** CI15321 (2n = 42), 1Ae-1(1D) substitution line; **b** 87-94-1 (2n = 42 + 2t), ditelosomic addition 1Ae-1L; **c** CI15322 (2n = 42), 1Ae(1D) substitution and 4DS·4DL-1Ae-1L translocation

GISH analysis revealed that one pair of complete *Ag. elongatum* chromosomes and one pair of wheat-*Ag. elongatum* translocation chromosomes are present in CI15322. The translocated chromosome has a small *Agropyron* chromosome segment translocated to the long arm of a wheat chromosome with an arm ratio (L/S) of 1.92. Based on this arm ratio, and in comparison with the C-banding pattern of the individual chromosomes of CI15322 with those of CI15321 and 87-94-1, the translocation probably involved chromo-

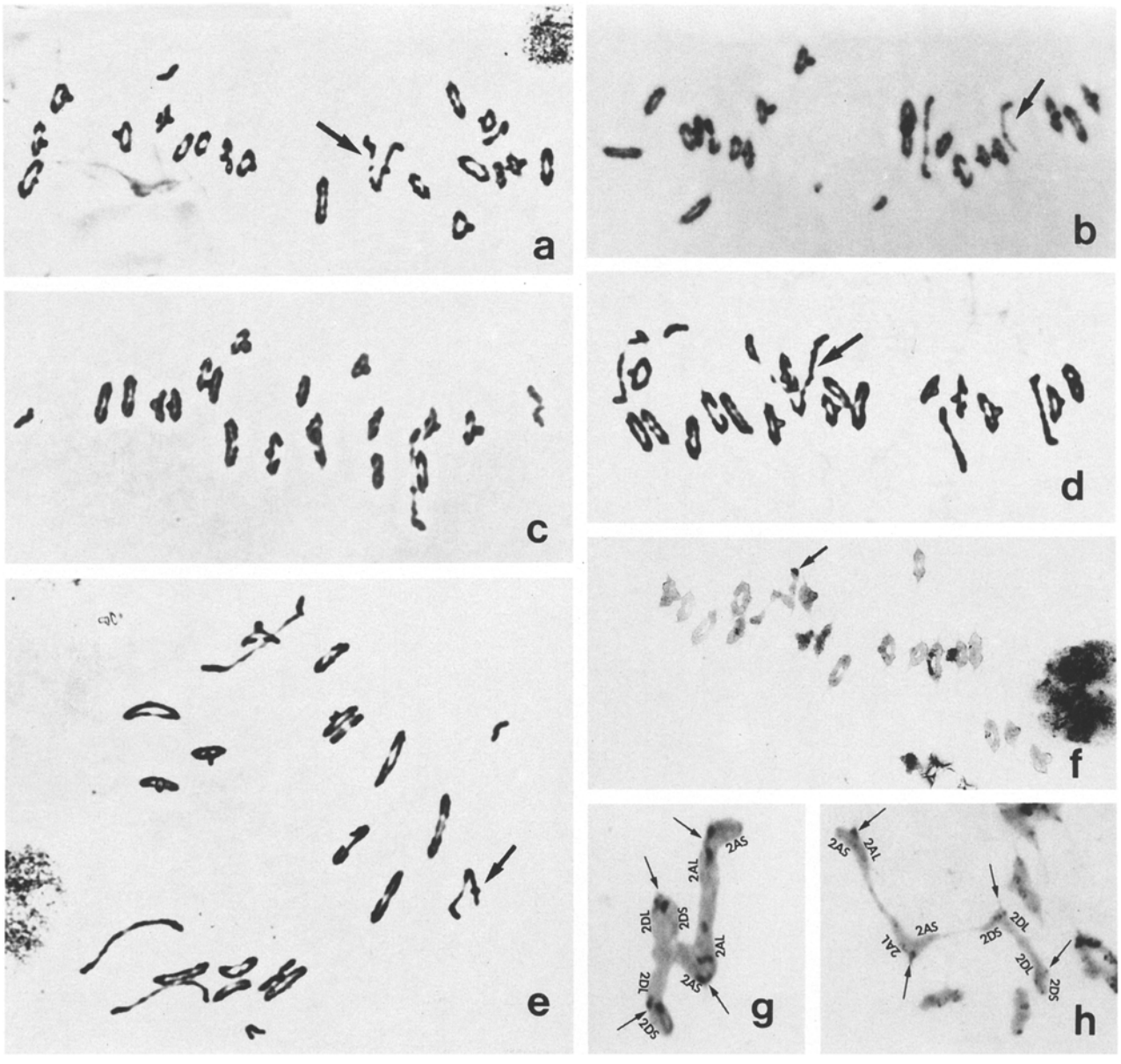

Fig. 2a–h. Metaphase I chromosome pairing in: **a** (CS nulli 1D-tetra 1B × CI15321)F_1, 1I + 19II + 1III (*arrow*); **b** (87-94-1 × CI15321)F_1, 1I + 21II, the heteromorphic bivalent is *arrowed*; **c** (CS mono 4D × C15322)F_1, 3I + 19II; **d** (CS nulli 1D-tetra 1B × CI15322)F_1, 1I + 19II + 1III (*arrow*); **e** (CI15322 × 87-94-1)F_1, 2I + 19II + 1III, the heteromorphic trivalent is *arrowed*; **f** in situ hybridization pattern of (CI15321 × CI15322)F_1, 19II + 1IV, using a ribosomal gene as the probe: note the location of ribosomal gene signal on 1Ae-2 in the quadrivalent (*arrow*); **g** N-banding pattern of the quadrivalent involving 2A/2D translocation (*arrows* point to the centromeres), **h** C-banding pattern of the quadrivalent involving 2A/2D translocation (*arrows* point to the centromeres)

some 4D of wheat. To verify the translocation, CI15322 was crossed with 'Chinese spring' monosomic 4D as female. The F_1 plants (2n = 41) showed 3I + 19II at MI (Fig. 2c). The three univalents were expected as 1D, 4D, and 1Ae-2, respectively. GISH analysis on meiotic chromosomes confirmed that the three univalents consisted of one complete *Agropyron* chromosome (1Ae-2), one wheat-*Agropyron* translocated chromosome (4D), and one wheat chromosome (1D). This experiment also indicated that the *Agropyron* chromosome segment attached to 4D has no homology with 1Ae-2 because they do not pair with each other.

The 1Ae-2 (1D) substitution was also confirmed by meiotic analysis of nulli 1D-tetra 1B × CI15322 F_1 plants (Table 1, also see Fig. 2d). In F_1 plants between CI15322 and 87-94-1, chromosomes paired as 2I + 19II + 1III. The telocentric chromosome of 87-94-1

Table 1. Chromosome pairing at meiotic metaphase I of crosses involving CI15321, CI15322, and 87-94-1

Crosses	Modal pairing configurations (percentage of cells observed)	Cells observed
CS nulli 1D-tetra 1B × CI15321	1I + 19II + 1III (56%) 2I + 20II(40%)	50
CS nulli 1D-tetra 1B × CI15322	1I + 19II + 1III (56%) 2I + 20II(40%)	50
87-94-1 × CI15321	1I + 21II[a] (85%)	20
CI15322 × 87-94-1	2I + 19II + 1III[b] (68%)	50
CI15321 × CI15322	19II + 1IV (82%)	50
CS monosomic 4D × CI15322	3I + 19II (70%)	50

[a] Including one heteromorphic bivalent involving one complete chromosome and one telocentric chromosome
[b] The trivalent was heteromorphic involving two complete chromosomes and one telocentric chromosome

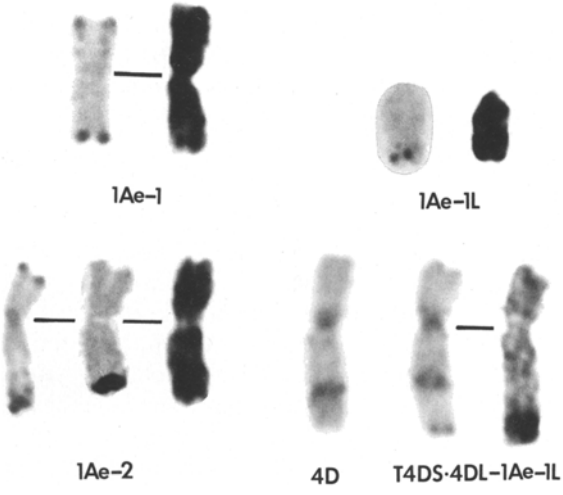

Fig. 3. C-banding and genomic in situ hybridization (GISH) patterns of the critical wheat, *Ag. elongatum* and wheat-*Ag. elongatum* translocation chromosomes in CI15321, 87-94-1, and CI15322. 1Ae-1 in CI15321: C-banding (left), GISH (right); 1Ae-1L in 87-94-1: C-banding (left), GISH (right); 1Ae-2 in CI15322: C-banding (left), ribosomal gene in situ hybridization (middle), GISH (right); 4D: C-banding; T4DS·4DL-1Ae-1L in CI15322: C-banding (left), GISH (right)

paired with two chromosomes as a heteromorphic trivalent (Fig. 2e). Based on the available evidence, the best explanation for this pairing configuration is as follows: the *Agropyron* chromosomes segment attached to 4D was derived from the distal part of the telocentric chromosome (1Ae-1L). The C-banding pattern supports this hypothesis because both 1Ae-1 and the translocated 4D have a similar telomeric C-band on their long arms (Fig. 3). The trivalents involved chromosome 1Ae-1L, the translocated 4D from CI15322, and a normal 4D from 87-94-1. The two univalents are 1D and 1Ae-2, respectively.

In the F_1 plants between CI15321 and CI15322, chromosomes paired as 19II + 1IV in 82% of the pollen mother cells (Table 1, also see Fig. 2f). If 1Ae-1 and 1Ae-2 are completely non-homoeologous to each other, the expected pairing configuration of this hybrid should be 1I (1Ae-2) + 19II + 1III (1Ae-1↔translocated 4D↔4D). The present data suggest that one arm of 1Ae-2 paired with the short arm of 1Ae-1, the quadrivalents involved chromosomes 1Ae-2↔1Ae-1↔translocated 4D↔4D. The meiotic samples of this hybrid were analyzed by in situ hybridization using the ribosomal genes as a probe. The ribosomal genes on 1Ae-2 in the quadrivalents were consistently located on the non-pairing arm (Fig. 2f). This result indicated that the short arm of 1Ae-2 pairs with the short arm of 1Ae-1 in the quadrivalent. The long arms of 1Ae-1 and 1Ae-2 apparently cannot pair with each other because the translocated 4D, which has the terminal segment from 1Ae-1L, does not pair with 1Ae-2 in F_1 plants between 'Chinese Spring' monosomic 4D and CI15322.

Table 2. Length (μm) of different chromosomes in CI15321, CI15322, and 87-94-1

Chromosome	Short arm	Long arm	Short arm + long arm	Arm ratio	% of 3B
3B (CI15321)	4.07 (0.62)[a]	5.64 (0.79)	9.71 (1.25)	1.39	100
1Ae-1 (CI15321)	2.59 (0.39)	2.87 (0.37)	5.46 (0.79)	1.11	56
1Ae-1L (87-94-1)		2.62 (0.30)			27
1Ae-2 (CI15322)	2.22 (0.33)	2.83 (0.38)	5.05 (0.61)	1.27	52
4DS·4DL-1Ae-1L (CI15322)	2.07 (0.23)	3.98 (0.55)	6.05 (0.75)	1.92	62
4D (CI15321)	2.20 (0.25)	3.40 (0.23)	5.60 (0.43)	1.55	58

[a] Standard deviation

In all crosses with CI15322, an extra quadrivalent was observed at MI. The frequency of this quadrivalent ranged from 5% to 20% in different crosses involving CI15322. Both N-banding and C-banding were performed on meiotic samples from different cross combinations involving CI15322. The results showed that the quadrivalents involved chromosome 2A and 2D of wheat (Fig. 2g and h). Based on the banding patterns of the quadrivalents, the homoeologous pairing between 2A and 2D always involved the short arms. This suggests that there is a reciprocal 2A/2D translocation in line CI15322 which involves the short arms of these two chromosomes.

In summary, the chromosome constitutions of the three WSMV-resistant lines can be described as follows:

(1) CI15321 is a disomic substitution line. Chromosome 1D is substituted by the *Ag. elongatum* chromosome 1Ae-1.
(2) 87-94-1 is a ditelosomic addition line. The telocentric chromosome is the long arm of 1Ae-1.
(3) CI15322 has a complete *Ag. elongatum* chromosome, 1Ae-2, that replaces chromosome 1D. The long arm of chromosome 4D in this line has an attached *Agropyron* chromosome segment that was derived from the terminal part of the long arm of 1Ae-1. This chromosome is designated as T4DS·4DL-1Ae-1L.
(4) The short arm of 1Ae-1 is homologous to the short arm of 1Ae-2. The long arms of 1Ae-1 and 1Ae-2 cannot pair with each other.
(5) CI15322 has a reciprocal 2A/2D translocation.

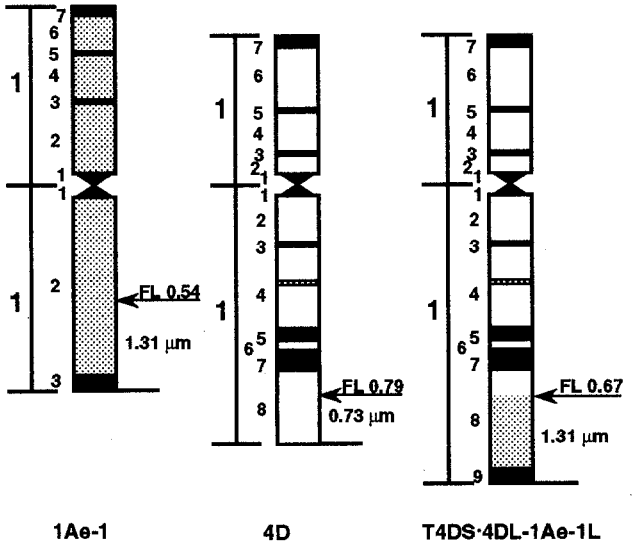

Fig. 4. Idiograms of chromosome 4D of CI15321, the *Ag. elongatum* chromosome 1Ae-1, and wheat-*Ag. elongatum* translocation chromosome T4DS·4DL-1Ae-1L (*arrows* point to the translocation breakpoints). The idiograms of 4D and T4DS·4DL-1Ae-1L are according to Gill et al. (1991)

Breakpoint of translocated chromosome T4DS·4DL-1Ae-1L

Chromosome measurement data are summarized in Table 2. Measurements on T4DS·4DL-1Ae-1L chromosomes after genomic in situ hybridization revealed that the labeled region consists of the distal 33% of the long arm of this chromosome. Based on the length of the long arm of T4DS·4DL-1Ae-1L (3.98 μm), the translocated *Ag. elongatum* chromosome segment has a size of 1.31 μm. This segment corresponds to 46% of the long arm of 1Ae-1. Therefore, the original break on 1Ae-1 is at a fraction length (FL) of 0.54 on the long arm (Fig. 4). Based on the calculation of the length of 4DL – (the length of long arm of T4DS·4DL-1Ae-1L – the length of the transferred *Ag. elongatum* chromosome segment), the size of the lost wheat chromosome segment of T4DS·4DL-1Ae-1L is 0.73 μm, and the original break on chromosome 4D is at a fraction length of 0.79 on the long arm (Fig. 4).

Discussion

P_3-19, from which CI15321 and CI15322 were derived, had two pairs of *Ag. elongatum* chromosomes, one relatively long and the other rather short. The two *Agropyron* chromosomes seem not to be homologous to each other, although the determination of whether they ever paired was not made (Sebesta and Bellingham 1963). The overall morphology of chromosome 1Ae-1 of CI15321 and 1Ae-2 of CI15322 are similar to the *Agropyron* chromosomes of P_3-19 described by Sebesta and Bellingham (1963). However, the short arm of 1Ae-2 is obviously homologous to the short arm of 1Ae-1 based on the chromosome pairing of F_1 hybrids between CI15321 and CI15322. This indicates that either 1Ae-1 or 1Ae-2, or both, were modified during the process of isolation of new WSMV-resistant germplasm from P_3-19.

Recent evidence of chromosome pairing suggested that *Ag. elongatum* is an autodecaploid and has seven groups of ten homologous chromosomes (Muramatsu 1990). Since the short arms of 1Ae-1 and 1Ae-2 pair regularly at MI, these two arms should belong to the same homologous group. Surprisingly, the C-banding patterns of these two arms are quite different. The long arms of 1Ae-1 and 1Ae-2 do not pair with each other at MI. Therefore, at least one of these two long arms could derive from a different homologous group.

Multivalents were also observed in P_3-19 and its hybrids with 'Wichita' wheat, but they did not involve *Agropyron* chromosomes (Sebesta and Bellingham 1963). These multivalents could be related to the 2A/2D translocation observed in CI15322, although their frequencies (1–4%) are relatively lower than those in the present study (5–20%).

Sebesta and Bellingham (1963) also found that only one pair of *Agropyron* chromosomes, possibly the shorter one, was involved in the genetic control of WSMV resistance in P_3-19. Since all three lines in the present study contain part or all of the arm 1Ae-1L, the major resistance gene(s) is probably located on the distal part of 1Ae-1L. To confirm this hypothesis, a new line with only chromosome T4DS·4DL-1Ae-1L should be isolated and tested for its disease resistance. This study is underway.

Although both CI15321 and CI15322 were highly resistant to WSMV and its vector (Martin et al. 1976; Pfannenstiel and Niblett 1978), minor differences in their reaction patterns were observed (Martin et al. 1976). Therefore, the possibility of the existence of minor gene(s) on 1Ae-2 or/and the short arm of 1Ae-1 still cannot be excluded.

The designation of chromosomes 1Ae-1 and 1Ae-2 was based on their spontaneous substitution for wheat chromosome 1D. The morphology and agronomic performance of CI15321 and CI15322 indicate that chromosome 1D is genetically compensated for by 1Ae-1 and 1Ae-2. These two *Agropyron* chromosomes, or at least one arm, belong to wheat homoeologous group 1. Conclusive evidence from protein or DNA markers is needed to further confirm this identification. Unfortunately, if the long arm of 1Ae-1 belongs to homoeologous group 1, chromosome T4DS·4DL-1Ae-1L will be a non-compensating translocation. However, since the missing 4DL segment has a size of only 0.73 μm, this loss of wheat chromatin is well-tolerated based on the agronomic performance of CI15322. Therefore, a line that has chromosome T4DS·4DL-1Ae-1L will have potential in wheat breeding for WSMV resistance.

The present study showed that GISH is extremely useful to detect alien chromatin and breakpoints in wheat-alien chromosome translocations. Chromosome banding analysis is necessary to identify the chromosomes involved in the translocations. In the present case, conclusive characterization of translocation T4DS·4DL-1Ae-1L would have been impossible without combining the aneuploid and chromosome pairing analyses. Therefore, the techniques of high resolution C-banding and GISH, combined with confirmatory aneuploid and chromosome pairing analysis, provide the most accurate and efficient method of cytogenetic analysis in plants.

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